Ecological succession drives the structural change of seed-rodent interaction networks in fragmented forests

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Abstract: While deforestation and fragmentation can cause massive species loss in forest ecosystems, forest regeneration can also drive successional changes in species composition. Although studies have sometimes documented the effects of these compositional changes on interspecific interactions, few studies have investigated changes in the structure of plant-animal networks. We investigated how interaction networks of assemblages of rodents and tree seeds changed with forest fragmentation and succession in a subtropical region. We compared seed-rodent interactions between 14 secondary forest patches that ranged in area from 2 to 58 ha, and from 10 to at least 100 years old, representing a successional gradient. We expected that deforestation and fragmentation would reduce seed production and diversify rodent communities, resulting in higher interaction strengths and connectivity, but weak nestedness (i.e., specialists interact with subsets of the species interaction of generalists). We measured the frequency of rodents eating and removing seeds (interaction strength) in each patch during 3 successive years, using seed tagging and infrared camera trapping, and calculated the properties of the seed-rodent networks. We found that the relative abundances of seeds and rodents changed with stand age not patch size, as did seed-rodent interactions: older patches produced more seeds, contained fewer individuals and species of rodents, and had seed-rodent networks with lower connectance and interaction strength, but higher nestedness. Connectance and interaction strength decreased with metabolic per capita seed availability (as measured by seed energy value); nestedness increased with seed richness, but decreased with rodent abundance. At species level, we found stand age and patch size showed significant effects on seed or rodent abundance of a few species. We also found seed coat thickness and starch contents had significant effects on network metrics. Our results suggest that during succession after deforestation, seed-rodent interactions in these sub-tropical forests change from a state dominated by high seed removal and highly connected seed-rodent networks to a state with more seeds and highly nested networks. From a management perspective of our study region, succession age, not fragment size, and network structure should be paid more attention so as to facilitate the restoration processes of degraded forests. Rodent management should be applied to protect native forest species and exclude incursive ones from farmlands and human residences at early succession stage.

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Running head: Succession and seed-rodent interactions

Title: Ecological succession drives the structure of seed-rodent interaction networks

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Abstract

Deforestation and fragmentation have been shown to trigger massive species loss in forest ecosystems. Although changes of species composition are expected to alter species interactions, existing studies have rarely investigated such changes in the context of plant-animal networks. In this study, we investigated the association of forest deforestation and fragmentation with interaction networks of assemblages of rodents and trees seeds in a subtropical forest region. We compared seed-rodent interactions between forest patches that ranged from 10 to at least 100 years old. We expected that deforestation and fragmentation would reduce seed production and diversify rodent communities, resulting in higher interaction strengths and connectivity, but weak nestedness. We tested these ideas by using seed tagging and infrared camera trapping to measure the frequency of rodents removing seeds (interaction strength) in 14 regrowth forest patches which formed a successional gradient during 3 successive years. We found that the relative abundances of seeds and rodents changed with stand age not patch size, as did their interactions: older patches produced more seeds, but contained fewer individuals and species of rodents. Consequently, seed-rodent networks in older patches had lower connectance and interaction strength, but higher nestedness. While connectance and interaction strength increased with rodent abundance, nestedness decreased; conversely, seed richness increased nestedness. Our results suggest that an early successional state dominated by seed production and removal was replaced by a more mature state with fewer seeds produced in less connected networks. Future studies should test whether it is a general finding that post-deforestation forest succession and community assembly restore network structure towards that found in old stands with weakened seed-rodent interactions.

INTRODUCTION

Many studies have demonstrated that habitat loss and fragmentation has huge negative effects on biodiversity (Aguilar *et al.*, 2006). One negative effect of fragmentation that has been reported concerns the breakdown of species interactions by habitat degradation, edge effects and fragment isolation and area (Magrach *et al.*, 2014). Recent studies have shown that mutualisms, such as pollination and seed dispersal, are sensitive to the negative effects of forest fragmentation (Aguilar *et al.*, 2006, Fortuna & Bascompte, 2006, Magrach *et al.*, 2014, Uriarte *et al.*, 2010). Although effects of anthropogenic disturbance on forest species richness and abundance have been widely explored, its consequences for species interactions have rarely been investigated.

Various ecological interaction networks have been investigated in literature, such as food webs, mutualistic networks (e.g., flower-pollinator and seed dispersal by birds) and bipartite antagonistic networks (e.g., plant-herbivore and host-parasite interactions) (CaraDonna *et al.*, 2017, Dattilo *et al.*, 2014, Neuhauser & Fargione, 2004, Schleuning *et al.*, 2011). The interests of many studies have largely lied in linking specific network measures to structure and stability of ecological communities or ecosystems. Two basic metrics for ecological networks are connectance (probability of realized interaction) and interaction strength (May, 1972). Strong interaction strength and high connectance in more diverse networks often decrease local stability of random ecological networks (May, 1972), while Thebault and Fontaine (2010) demonstrated that a highly connected architecture promoted community stability in mutualistic networks with empirical structure. Weak interaction strength has been widely accepted as a potential mechanism for maintaining diversity and stability (Berlow, 1999, Neutel *et al.*, 2002). In recent decades, nestedness (i.e., specialists

interact with proper subsets of the species interaction of generalists) and modularity (i.e., compartmentation of species interactions) have been identified as common architectures in ecological networks and could promote stability (Bascompte & Jordano, 2007, Bascompte *et al.*, 2003, Bascompte *et al.*, 2006, Gilarranz *et al.*, 2017, Olesen *et al.*, 2007, Rohr *et al.*, 2014). Besides above ones, other metrics have been and may continue to be investigated, such as mixture of interaction types (Allesina & Tang, 2012, Mougi & Kondoh, 2012), omnivory (McCann & Hastings, 1997) and non-monotonicity (Yan & Zhang, 2014). Therefore, network metrics could be used to test how human disturbance affects structure and stability of natural communities.

Seed-rodent networks are an important interaction network type in forest ecosystems, and they play an important role in the maintenance of biodiversity and ecosystem services (Thayer & Vander Wall, 2005, Zhang *et al.*, 2016a). In nature, a majority of plant seeds are finally consumed by rodents, but a small proportion of them survive from predation by rodents and develop into seedlings (Vander Wall, 2010). Consequently, interactions between tree seeds and rodents vary between being predatory and mutualistic (Garzon-Lopez *et al.*, 2015, Theimer, 2005, Xiao & Zhang, 2016, Zhang *et al.*, 2016b). Both the abundance and functional traits of rodents and seed species are key factors in the formation of mutualistic and predatory interactions between seeds and rodents (Garzon-Lopez *et al.*, 2015, Wang *et al.*, 2014, Zhang *et al.*, 2015). Previous studies have evaluated specific seed-rodent interactions in semi-natural enclosures (Wang *et al.*, 2014, Zhang *et al.*, 2016b), but never in field conditions because of a lack of methods for measuring seed-rodent interaction strength. Therefore, little is known about the structure of natural seed-rodent interaction networks and how they could be affected by human disturbances such as forest deforestation and fragmentation.

Many studies have found that deforestation significantly affects species composition and abundance (Benchimol *et al.*, 2017, Brook *et al.*, 2003, Fisher & Wilkinson, 2005). Deforestation has been shown to decrease seed species richness and abundance by removing large trees (Benchimol *et al.*, 2017, Laurance, 1999). Deforestation or fragmentation also creates suitable open habitats for small rodents, increasing both species richness and abundance. Correspondingly, several studies found that rodent abundance increases with forest disturbance (Duntan & Fox, 1996, Shenko *et al.*, 2012). These contrasting changes of seed-predator/disperser abundance and species richness would be expected to alter the strength of seed-rodent interactions (i.e., the frequency of seed removal by rodents). Outside of a fragmentation context, studies have demonstrated that seed availability, predator satiation or dispersal behavior, can affect the strength of interactions between seeds and rodents (Xiao *et al.*, 2013, Yi *et al.*, 2011). Optimal foraging theory and optimal diet selection theory describe potential mechanisms (Bolnick *et al.*, 2010, Emlen, 1966). Based on these theories, one may expect that in more disturbed or younger forest patches, seed-rodent interactions are stronger due to relatively low seed availability for rodents, so that the connectance of seed dispersal networks is higher with lower nestedness.

This study aimed to determine how forest succession and fragmentation affect seed-rodent interaction networks. Specifically we tested the following predictions: (1) Rodent species richness and abundance decrease with the size and age of forest patches; (2) interaction strength and connectance decrease, but nestedness increases with the size and age of forest patches; (3) interaction strength and connectance decrease, and nestedness increases with increase of seed availability. Our approach was to compare seed removal rates across 14 patches of subtropical forest in the

Dujiangyan region, Sichuan Province, southwest China, that differed in age and size.

MATERIALS AND METHODS

Study site

The study was performed in the deforested and fragmented subtropical evergreen broad-leaf forest, located in the Dujiangyan region (altitude 600-1,000 m, 31°04′ N-31°05′ N, 103°42′ E -103°43′ E) of Sichuan Province, southwest China. It lies in the transition zone between the Qinghai-Tibetan Plateau and the plains of Chengdu, and is part of the mountains west of the Sichuan Basin. The climate is subtropical, with a mean annual temperature of 15.2 °C, and annual precipitation of 1200-l800 mm. Peak precipitation occurs at the highest elevations within our site and declines with elevation. The Dujiangyan region is a hotspot of biodiversity in China.

Our study was conducted in 14 forest patches annually from 2014 to 2017. Most of forest was cleared in the 1980s-2000s, and subsequently forest fragments of 2.0 to 58.0 ha were allowed to regrow on hilltops while flatter areas were maintained in cultivation or became roads (Zhao *et al.*, 2016). These forest patches were classified into three kinds based on stand ages, and also varied in patch sizes. Experiments were conducted in 14 forest patches (labeled as A, B1, B2, C, D, F, H, K, L, M, R, S, U and V; Fig. 1; Table 1). Forests in patch B1 and patch B2 are at least 100 years old, and we refer to them as primitive, because of their age and protection from the nearby Banruosi Temple. The other forest patches have undergone extensive logging and destruction in the 1980s-2000s and represent early or middle succession stages. The stand age was categorized into early, middle and primitive forests because the accurate year of deforestation was unknown (Table 1).

Table 1. The 14 experimental patches in the Banruosi Experiment Forest in the Dujiangyan region of Sichuan province, China. The capital letters indicate plot codes.

Stand ages (year)	Patch sizes (ha.)					
Early stands (10 ~ 20 years old)	D(22.99)	L(41.89)	R(20.23)	C(4.20)	A(2.68)	U(2.85)
Middle stands (20 ~ 40 years old)	F(17.63)	K(57.51)	S(16.18)	M(5.23)	H(6.05)	V(3.75)
Primitive stands (≈ 100 years old)	B1(40.12)	B2(45.34)				

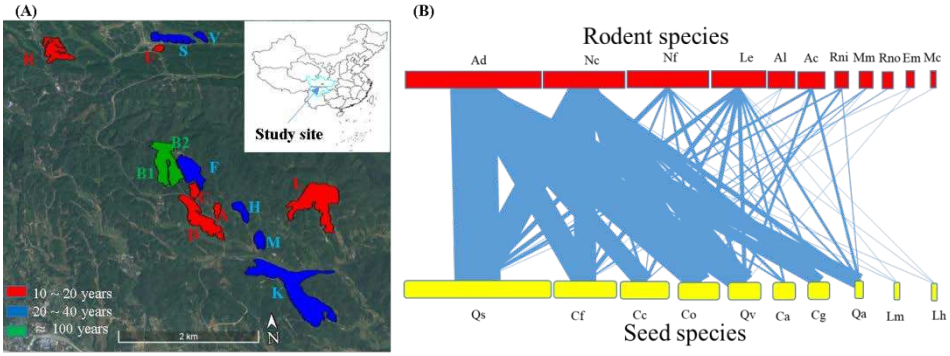

Fig. 1. The 14 experimental plots with different size and succession age (A) and aggregated rodent-seed interaction network of all the plots over three years (B). In the interaction network, the width of rectangles indicates the relative abundance of rodent or seed species, and the thickness of links indicates the relative interaction strength between each pair of rodent and seed species. Abbreviation of rodent species: Ad-*Apodemus draco*, Nc-*Niviventer confucianus*, Nf-*N. fulvescens*, Le-*Leopoldamys edwardsi*, Al-*A. latronum*, Ac-*A. chevrieri*, Rni-*Rattus nitidus*, Mm-*Micromys minutus*, Rno-*R. norvegicus*, Em-*Eothenomys melanogaster* and Mc-*Musmus culus*, respectively. Abbreviation of seed species: Qs-*Quercus serrata*, Cf- *Castanopsis fargesii*, Cc-*C. ceratacantha*, Co-*Camellia oleifera*, Qv-*Q. variabilis*, Ca-*Choerospondias axillaris*, Cg-*Cyclobalanopsis glauca*, Qa-*Q. acutissima*, Lm-*Lithocarpus megalophyllus* and Lh-*L. hancei*, respectively.

In the study site, the common tree species include *Lithocarpus hancei*, *Quercus acutissima*, *Q. serrata*, *Q. variabilis*, *Cyclobalanopsis glauca*, *L. megalophyllus*,

168 *Choerospondias axillaris*, *Castanopsis fargesii*, *C. ceratacantha* and *Camellia*
169 *oleifera*. We recorded 11 sympatric rodent species in this region, including South
170 China field mice (*Apodemus draco*), Chevrier's field mice (*A. chevrieri*), Sichuan
171 field mice (*A. latronum*), Edward's long-tailed rats (*Leopoldamys edwardsi*), Chestnut
172 rats (*Niviventer fulvescens*), Chinese white-bellied rats (*N. confucianus*), Norway rats
173 (*Rattus norvegicus*), Himalayan rats (*R. nitidus*), Pere David's vole (*Eothenomys*
174 *melanogaster*), Harvest mice (*Micromys minutus*) and House mouse (*Musmus culus*)
175 (Xiao *et al.*, 2013). These rodent species either feed on tree seeds such as nuts and
176 acorns or hoard them. Thus, rodent seed dispersers potentially play a significant role
177 in forest seed regeneration as seed dispersers. All recorded rodent species are
178 nocturnal.
179
180 **Sampling design**
181 *Seeds*
182 Seed fall was measured using seed traps made of Vinylon (New Agricultural Net
183 Factory, Dujiangyan, China, mesh size =2 mm) (Zhang *et al.*, 2016b, Zhao *et al.*,
184 2016). Each trap sampled a square 1 × 1 m area (Fig. S1A). In late August 2014, we
185 set up 178 traps suspended 0.8-m above the ground using bamboo or trunk posts to
186 prevent access by terrestrial vertebrates. To allow for differences in patch sizes, 3-7
187 seed traps were placed in a plot, in 2 or 4 sampling lines with a spacing of 10 m
188 between adjacent traps. In each year, we collected fallen seeds every 2 weeks from
189 early September to late December when seeds became mature. Seed rain from each
190 seed trap was put separately into an envelope and marked with a unique code. Seeds
191 were transported back to the lab and oven-dried (Xinkangyida Technology
192 Development Co. Ltd, model DH-101-3BS, Beijing, China) at 60^{o}C for 12 hours.

After drying, seeds were weighed, counted, identified to species, and any insect infection noted. During the peak period of seed rain, fresh and intact seeds of each species were collected for use in seed-dispersal experiments.

Rodents

We used wire live traps (30 × 13 × 12 cm), baited with fresh chestnuts to trap small rodents (Zhao *et al.*, 2016). We placed them into 4×10 grids with intervals of 10 m in each plot (Fig. S1B) for five consecutive nights during October to November each year. Traps were placed at 15:00 - 17:00 hours in the afternoon and were checked at 7:00 - 9:00 hours the next morning. All captured animals were weighed and identified to species, sex and reproductive status (females pregnant, lactating or not; males with testes descended or not). Individuals were also marked with unique and distinguishable patterns on their back with wine-red human hair dye (Gu *et al.*, 2017) and then released *in situ*. Color labeling was used for mark-recapture analysis of abundance and to identify individuals on infrared cameras and determine if they ate or removed seeds at the seed stations (Gu *et al.*, 2017, Zhao *et al.*, 2016). Procedures for capturing and raising animals were in accordance with the regulations of the Institute of Zoology, Chinese Academy of Sciences.

Seed-rodent interactions

Seed removal trials were carried out from August 2014 to April 2017 in the Banruosi Experimental Forest and its periphery (700–1000 m ASL, 31°04′ N, 103°43′ E) in the Dujiangyan region. We used infrared (IR) cameras to monitor large and medium-sized rodent species, and measuring seed caching and pilferage(Jansen *et al.*, 2002). We applied a modified seed tagging method (Forget, 1990, Xiao *et al.*, 2006, Zhang & Wang, 2001) and IR cameras to track the removal and fate of individual

seeds by rodents and thus measure the interaction strength between rodents and tree seeds, as follows (also see: Zhao et al. 2016, Gu et al. 2017). We selected seeds of 10 common tree species: *L. hancei*, *Q. acutissima*, *Q. serrata*, *Q. variabilis*, *C. glauca*, *L. megalophyllus*, *C. axillaris*, *C. fargesii*, *C. ceratacantha*, and *C. oleifera*. The seed rain periods of these tree seeds generally overlapped, with only minor variation in peak time (Zhao *et al.*, 2016). During the time when various seeds were mature, fresh and intact seeds were collected from the ground or trees outside of the experimental patches, and air dried in a cool place.

We labeled seeds using the tagging methods of Zhao *et al.* (2016). A 0.5-mm diameter hole was drilled through the husk near the germinal disc of each seed. Though the cotyledons were partly damaged (except for *L. hancei* nuts), the embryo remained intact and was capable of germinating. A small, light white plastic tag (3.6 × 2.5 cm, < 0.1 g) with different shapes was tied through the hole using a thin steel wire 10 cm long (Figs S1C, D). Each weighed seed was given a unique code by writing on the tag using a fine point metal-pen. When rodents buried the seeds in the soil, the plastic-tags were often left on the surface, making them easy visually relocate.

In November or December of 2014, 2015 and 2016, three seed stations 30-m apart were haphazardly established in each stand. Depending on the availability of seed species in each patch, 2-8 seed species were placed at a single station, and each species including 10 tagged seeds with unique codes reflected in different tag shapes, spaced evenly on the soil surface within 1-2 m^2 (Fig. S1C, D). IR camera traps (Ltl -5210A, Zhuihai Ltl Acorn Electronics Co., Ltd, Zhuihai, China) were tied to a tree adjacent to each seed station (0.4-0.7 m high) and set on video record mode (Video Size: 640 ×480； PIR sensitivity: High; Video Length: 20 s; Trigger Interval: 0 s) to

243 monitor seeds removed or eaten by small rodents (Fig. S1E, F). The day following
244 seed release, we checked the tagged seeds at each station to record seeds as being
245 removed or eaten. We then replaced the camera memory card, removed all remaining
246 seeds, and released new seeds for another round. This was replicated for three
247 consecutive days. Thus, we released 90 seeds per tree species per forest patch in each
248 of 3 years, and 13,830 seeds in total. We randomly searched a 25-m radius around
249 each station with equal effort (2-3 hours by two people for each plot visit), and record
250 the fate of the tagged seeds or whether seeds were missing with unknown fate. In the
251 lab, we systematically analyzed the video recordings (all capacity 537.3 gigabytes)
252 and identified rodent and seed species for each interaction.
253
254 **Data analysis**
255 *Measures of seeds and rodents*
256 Species richness of seeds (SR) was measured as the number of species observed in
257 each forest patch. Seed density (D) (m^{-2}) was calculates as the Total number of seeds
258 collected (No.) divided by the Total area of seed collector (m^2). Seed abundance (SA)
259 was measured as the total number of seeds produced by a patch. Metabolic seed
260 abundance (estimated by the seed calorific value per seed individual, MSA) was
261 calculated as: $\mathrm{MSA} = (\sum_{i=1}^{s} n_i CV_i)/S$, where S = the number of seed species; n_i= the
262 number of a given seed species i; CV_i = the average seed calorific value of a given tree
263 species i.
264 Species richness of rodents (RR) was measured by number of species observed in
265 each forest patch. Rodent abundance (RA) was estimated using the minimum number
266 alive (MNA) by the live trapping method described above for each plot and year.
267 Metabolic rodent abundance (the sum of metabolic-scaling body mass from each

rodent species each year, MRA) was calculated as: $\mathrm{MRA} = \sum_{i=1}^{S} n_i BM_i^{0.75}$, where S = the number of rodent species; n_i= the population size (here MNA) of a given rodent species i; $BM_i^{0.75}$ = the average metabolic-scaling body mass of a given species i. Per capita seed availability (PCSA): PCSA=SA/RA. Metabolic per capita seed availability (MPCSA): MPCSA= MSA/MRA (Xiao *et al.*, 2013).

Network measures

Among various network measures, we only considered several measures that are mostly related to structure and interaction strength of seed-rodent interactions in this study. Optimal diet theory predicts food availability can induce diet expansion or shifting, thus we chose connectance and links per species as the first set of network metrics to quantify the probability of interactions in each seed-rodent network. Changes in connectance and links per species should reflect the degradation or restoration of seed predation and dispersal function in forests. Connectance was measured by the proportion of realized links in a network, and the number of links per species was measured by the mean number of interaction links per species (Dunne *et al.*, 2002). The second set of network metrics quantifies nested architecture including nestedness and weighted nestedness. The latter takes into account the weight of the interaction strength (Galeano *et al.*, 2009). They were chosen because they are related to network stability (Bascompte *et al.*, 2003, Burgos *et al.*, 2007) and also reflect the structure of seed-rodent interactions as rodents, as generalists, might shift their diets as species composition changes. The last network metric is interaction strength (IS) between seed and rodent species, which is a direct measure of seed dispersal and predation by rodents, calculated as IS = overall number of seeds eaten and removed by rodents divided by the total number of tagged seeds released ×100% (Vazquez *et al.*, 2005). The *bipartite* package was used for calculation of network measures in the R 3.3 program (R

293 Development Core Team, 2014).

294 *Statistical analysis*

295 To identify the associations of post-deforestation succession and fragmentation with
296 seed-rodent interactions, we used linear mixed models to test: (1) The degree to which
297 stand age and patch size explained variation in the different species indices of seeds and
298 rodents (SR, SA, MSA, RR, RA, MRA, PCSA or MPCSA) across the 14 patches, with
299 year as a random variable. (2) The degree to which stand age and patch size explained
300 variation in the different network metrics (connectance, links per species, nestedness,
301 weighted nestedness and interaction strength), with year as a random variable. (3) The
302 degree to which species indices explained variation in network metrics, with year as a
303 random variable. The response variables were log-transformed to meet assumptions of
304 the statistical models if necessary. All linear mixed models were performed by *lme4*
305 and *lmerTest* in the R 3.3 program (R Development Core Team, 2014). We were not
306 able to do standard structural equation modeling analysis from stand age to network
307 metrics via abundance/richness of rodents/seeds because stand age of forest patches
308 was not a continuous variable.

309

310 **RESULTS**

311 **Forest stand age, size and species richness/abundance**

312 Rodent species richness ranged from 1 to 6 species, and rodent abundance ranged 3
313 to 19 individuals across the 14 forest patches. Rodent species richness ($F_{2, 33} = 9.97$, P
314 < 0.001), and rodent abundance ($F_{2, 33} = 9.77$, $P < 0.001$) or MRA ($F_{2, 33} = 4.59$, P
315 $=0.017$; Fig. 2; Table S1) significantly decreased with stand age. Seed species richness
316 ranged from 1 to 7 species, and seed abundance ranged 0.72 to 63.88 seeds across the
317 14 forests. Stand age had a significant positive association with seed species richness

($F_{2, 33}$=18.25, P < 0.001), but no significant association with seed abundance ($F_{2, 31}$ =0.81, P = 0.452) or MSA ($F_{2, 31}$ = 1.97, P =0.157; Fig. 2; Table S1). Stand age had a significant positive association with PCSA ($F_{2, 31}$=3.91, P = 0.031) and MPCSA ($F_{2, 31}$ =7.33, P =0.002; Table S1). Patch size had no significant association with species richness or abundance of either rodent or seed species (all P >0.05).

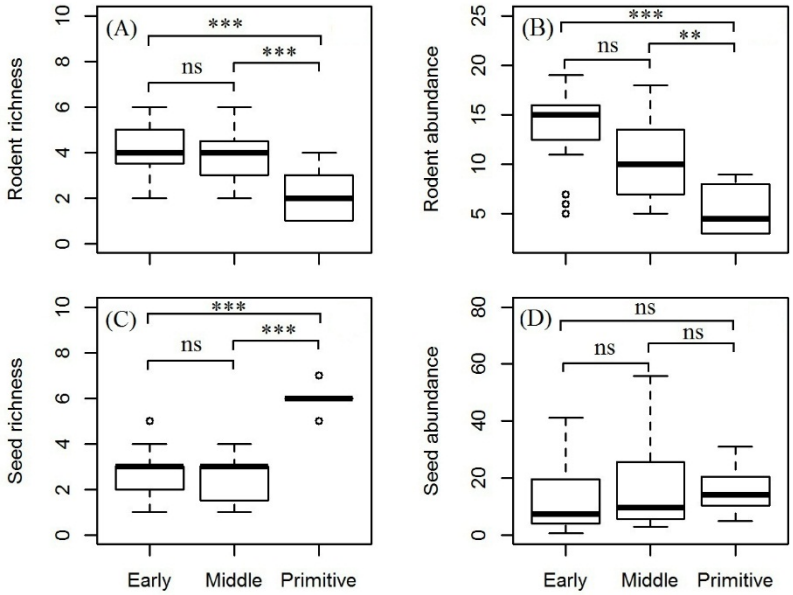

Fig. 2. Relationship between stand age and species richness and abundance of rodents (A, B) and seed richness and abundance (C, D). *, **, *** indicate P < 0.05, 0.01, 0.001, respectively, and ns indicates non-significant effect (P > 0.05). The bottom and top limits of each box are the lower and upper quartiles, respectively; the horizontal black band within each box is the median; and error bars equal ±1.5 times the interquartile range.

Forest stand age, size and network metrics

Connectedness ranged from 0.44 to 1, interaction strength ranged 0.07 to 1, and nestedness ranged 0 to 35.32 across the 14 forest patches. Stand age had significant negative associations with connectance ($F_{2, 31}$=3.93, P = 0.030) and interaction

strength ($F_{2, 31}$=3.82, P = 0.033; Fig. 3 and 4; Table S1). Stand age had a significant positive associations with nestedness ($F_{2, 22}$=8.05, P = 0.002; Fig. 3C and 4; Table S1). There were no significant associations of stand age on links per species or weighted nestedness (all P > 0.05; Table S1). Patch size had no significant associations with any network metric examined (all P >0.05; Table S1).

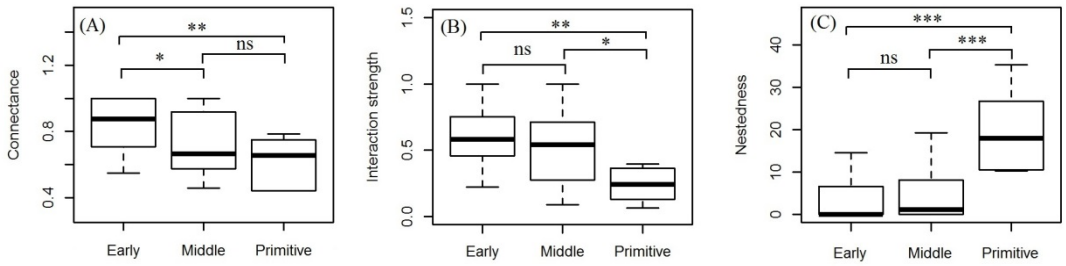

Fig. 3. Relationship between stand age and network metrics. *, **, *** indicate P < 0.05, 0.01, 0.001, respectively, and ns indicates non-significant effect (P > 0.05). The bottom and top limits of each box are the lower and upper quartiles, respectively; the horizontal black band within each box is the median; and error bars equal ±1.5 times the interquartile range.

Species abundance/richness and network metrics

Rodent abundance showed significant positive associations with connectance (t=2.158, P =0.039) and interaction strength (t=2.430, P =0.021), and a significant negative association with nestedness (t= -2.251, P =0.035; Fig. 4; Table S2). MRA had a significant positive association with interaction strength (t=2.403, P =0.022; Fig. 4; Table S2).

Seed richness had a significant positive association with nestedness (t=3.033, P =0.006) (Fig. 4; Table S2). MSA showed significant positive associations with weighted nestedness (t=4.408, P <0.001) and a significant negative association with connectance (t= -3.274, P =0.002; Fig. 4; Table S2). PCSA had no significant

associations on network metrics examined (all P >0.05; Fig. 4; Table S2). MPCSA had significant negative associations with connectance (t=-2.282, P =0.039) and interaction strength (t= -2.361, P =0.024; Fig. 4; Table S2).

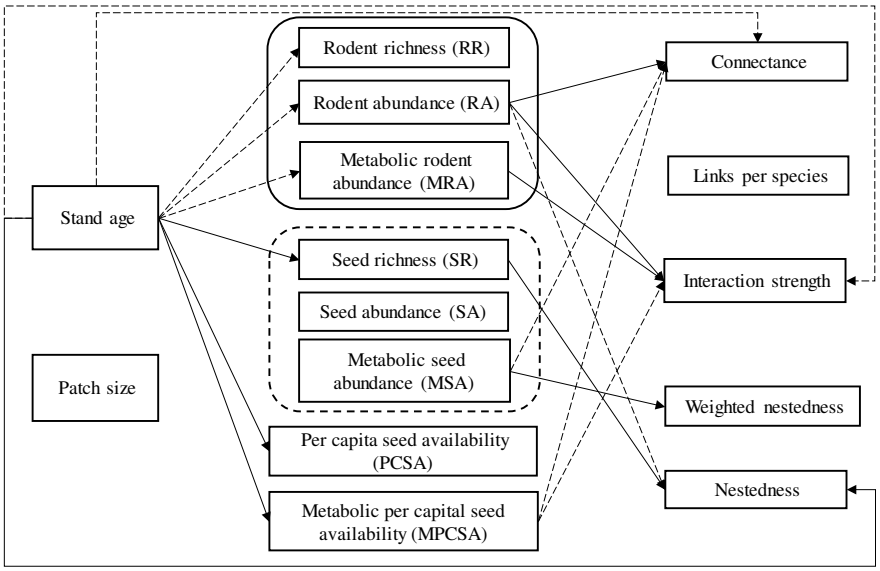

Fig. 4. Relationship of stand age and patch size with network metrics via species indices of rodents and seeds. Solid black lines represent significant positive associations, and dotted black lines represent significant negative associations. Solid line box represent rodent species indices, and dotted line box represent seed species indices. PCSA= SA/ RA; MPCSA= MSA/ MRA.

DISCUSSION

Deforestation or fragmentation can cause substantial change in species composition and abundance of forests (Brook *et al.*, 2003, Duntan & Fox, 1996, Fahrig, 2003). However, the consequences of such changes for interaction networks in ecosystems and communities are largely unknown. By using a combination of seed tagging and IR camera tracking, we were able to measure the interaction strength between seeds and rodents, and therefore, to quantify the impacts of human deforestation on the mutualistic relationship between plants and their seed dispersers.

We found that tree seed-rodent network metrics changed significantly with stand age (regrowth time since deforestation), but not with fragment patch size. In younger forest patches, interaction strength was stronger and nestedness was lower than in either older patches or primitive stands. These results suggest changes in network structure were mediated by changes in seed and rodent species richness and abundance, generally supporting the idea that seed availability to rodents changes the structure of seed-rodent networks. Because network metrics are important indicators for diversity and stability of ecosystems, the network architecture favoring stability fundamentally differs between trophic and mutualistic networks (Thebault & Fontaine, 2010). Our results provide new insights into the relationship between diversity and stability in forest ecosystems, and have implications for restoring degraded ecosystems.

Several previous studies indicated that species richness and diversity of small mammals were higher in young stands than old growth areas (Duntan & Fox, 1996, Sullivan *et al.*, 2000). This might be because deforestation creates open habitats with more grass seeds that benefit small rodents (Fisher & Wilkinson, 2005). Our results are generally consistent with these observations. We found in younger stands, rodent species richness and abundance (or metabolic rodent abundance) were higher, but seed species (or tree species) richness and abundance were lower (Fig. 2, 4; Table S3), supporting our Prediction 1. In our study region, deforestation mainly happened in 1980s-1990s, and many large trees like *Q. variabilis*, *C. fargesii* and *Cerasus pseudocerasus* were cut. In young stands, *Q.serrata* was the dominant tree species. With forest protection during the last three decades, the forest composition has begun to recover. Bird species are also an important component of the plant-animal interaction network (Gleditsch & Carlo, 2011). In our study site, few bird species (e.g.

400 *Garrulus glandarius*) were found to disperse seeds, and only in some patches (Zhao *et*
401 *al.*, 2016). Because of the sparsity of bird-seed interactions, we did not analyze them
402 further.

403 Human disturbance may impact species interactions involved in seed dispersal in a
404 variety of ways. For example, Wright and Duber (2001) reported that poachers and
405 habitat fragmentation indirectly altered the spatial pattern of seed dispersal, seed
406 predation, and seedling recruitment in the palm *Attalea butyraceae* in central Panama
407 when humans disrupted mammal communities. Aguilar *et al.* (2006) found a large and
408 negative effect of fragmentation on pollination and plant reproduction. Spotswood *et*
409 *al.* (2012) demonstrated that the presence of invasive fruit-bearing plants and
410 introduced frugivores altered seed dispersal networks, and found that the patterns of
411 alteration depended on both the frugivore community and the relative abundance of
412 available fruit. In plant-herbivore and host-parasitoid food webs, network structure
413 was altered by habitat fragmentation, with different metrics such as connectance,
414 vulunerablity and generality being affected depending on interaction type (Valladares
415 *et al.*, 2012). However, the effects of human activities such as deforestation on
416 seed-rodent interaction networks are poorly understood (Zhao *et al.*, 2016). We found
417 that the interaction strength and connectance were larger but nestedness was smaller
418 in younger stands, as compared older stands, supporting our Prediction 2. Our results
419 suggest that forest succession after deforestation would increase ecosystem stability
420 according to the previous studies that nestedness (Bascompte *et al.*, 2003, Bascompte
421 *et al.*, 2006, Pawar, 2014, Rohr *et al.*, 2014) and weak interactions (Berlow, 1999,
422 Neutel *et al.*, 2002) enhanced the stability of networks.

423 Habitat fragmentation has been reported to affect species interactions and then
424 network structure (Fahrig, 2003). The components of fragmentation generally include

changes in fragment size, isolation, edge effects and habitat degradation (Fahrig, 2003, Magrach *et al.*, 2014). Recent studies suggest that mutualisms, such as pollination and seed dispersal, were more sensitive to the negative effects of forest fragmentation than antagonisms, such as predation or herbivory (Aguilar *et al.*, 2006). Applying meta-analytical techniques, Magrach *et al.* (2014) demonstrated that the effects of fragmentation on mutualisms were primarily driven by habitat degradation, edge effects, and fragment isolation, with little effect of fragment size. Dattilo *et al.* (2015) found that fragment size did not affect the topological structure of the individual-based palm-pollinator network. However, Aguirre and Dirzo (2008) reported pollinator abundance was negatively affected by fragment size. In our study, we did not find significant effects of fragment size on the species richness and abundance or network metrics. This was likely because isolation had little effect for rodents and seeds. In our study area, the fragmented forests were isolated by the small and narrow farmlands or roads in the valleys. Small rodents can easily move across these farmlands, and dispersing seeds among patches.

Most mutualistic networks may be shaped by differences in species abundance among interacting species (Vazquez *et al.*, 2005, Verdu & Valiente-Banuet, 2011). For example, Dattilo *et al.* (2014) showed that the difference in abundance among ants on vegetation partially explained the network structure of mutualistic interactions and that the difference was independent of ant species compositions: abundant ant species generally interacted with more plant species. Gleditsch and Carlo (2011) suggested that bird abundance showed a strong positive association with *Lonicera* fruits. Consequently, the changes of animal and plant abundance were important factors in determining the plant-animal interaction network structure. For seeds and rodents, interaction strength may be affected by many factors, such as seed abundance, rodent

450 abundance, or seed availability (Schleuning *et al.*, 2011, Xiao *et al.*, 2013). Our study
451 demonstrated that rodent abundance had significant positive associations with both
452 connectance and interaction strength, but a significant negative association with
453 nestedness. Our study also showed that metabolic rodent abundance (MRA) had a
454 significant positive association with interaction strength, metabolic seed abundance
455 (MSA) had a significant negative association with connectance, and metabolic per
456 capita seed availability (MPCSA) had significant negative association with
457 connectance and interaction strength (Fig. 4; Table S2). These observations also
458 supported the predictions of optimal foraging theory and optimal diet selection theory
459 that interaction degree or diet breadth would increase because of stronger competition
460 for food resources with fewer seed resources or more predators (Araujo *et al.*, 2008,
461 Bolnick *et al.*, 2010, Emlen, 1966).
462 Several studies quantitatively assessed interaction strength between tree seed
463 species and rodent species by using semi-natural enclosures, and found functional
464 traits of seeds and rodents played a significant role in the formation of mutualism and
465 predation of the seed-rodent dispersal system (Wang *et al.*, 2014, Zhang *et al.*, 2015).
466 Zhang *et al.* (2015) found under enclosure conditions, large-sized rodents have
467 mutualistic or predatory interactions with both large- and small-sized seed species, but
468 small-sized rodents interacted with only small seed species. Zhang *et al.* (2016b)
469 provided evidence that the seed fates caused by hoarding behavior of rodents were
470 largely determined by trade-off-related seed traits (nutritional traits, coat thickness
471 and tannin content) and rodent body mass, and not by the phylogenetic relations of
472 species. In this study, we did not focus on the effects of functional traits, but we did
473 find similar results. For example, we showed that *A. draco* (abundant, small-sized
474 rodents) had more links with tree species such as *Q. serrata* (abundant, thin-coated

seeds), *C. fargesii* (small seeds with thin seed coat, low tannin content), but less links with trees like *C. axillaris* (thick seed coat). *N. fulvescens* and *N. confucianus* (large rodents) had more links with *Q. serrata*, *Q. serrata* (large seeds, high caloric value per seed but high tannin content) and *C. oleifera* (small seeds, high caloric value per seed and low tannin content) (X. F. Yang. unpubl. data). Rodents usually have generalized diet, and could establish links with dozens of plant seed species. On the other hand, a seed could also have links with various rodent species.

Robust estimates of the actual number of interactions (links) within diversified ecological networks require adequate sampling effort that needs to be explicitly gauged (Jordano, 2016). Biodiversity sampling is a labor-intensive activity, and sampling is often not sufficient to detect all or even most of the species present in an assemblage (Gibson *et al.*, 2011). Many previous studies focused on the interaction between plants and pollinators (CaraDonna *et al.*, 2017) or frugivorous birds (Schleuning *et al.*, 2011), but few have considered the interaction between plant fruits (seeds) and small mammals in natural conditions (but see (Gu *et al.*, 2017, Jansen *et al.*, 2012, Zhao *et al.*, 2016). One reason is that it is difficult to identify the seed-rodent interactions at an individual or species level. A combination of seed tagging and IR camera tracking allowed us to quantify seed-rodent interactions. However, our methods still have some limitations. Occasionally, a small proportion (3.7%) of rodents could not be identified due to their quick movement or failure of cameras. In the future, to clearly and more efficiently determine the individual relationship between seeds and rodents, it is necessary to use passive integrated transponder (PIT) tags to identify seeds and rodents (Shenko *et al.*, 2012). More detail ecological parameters of both rodents and seeds, such as rodent individual behavior and seed dispersal, storage, germination and survival, should be further analyzed and

researched in seed-rodent interaction networks to improve forest ecosystem management.

Our results highlight that forest succession after deforestation played a significant role in determining network structure, which may affect diversity and stability of seed-dispersal in fragmented ecosystems. Therefore, to facilitate the restoration processes of degraded forests, it is necessary to protect old-growth forests that provide seed sources, and reduce human disturbances (such as cutting, grazing and farming). Human intervention may be necessary if rodent density is too high, or seed source is too low. In such conditions, it would likely be beneficial to supply external seed resources by planting large trees or spraying seeds, and by managing the abundance of small rodents.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Statistical results from linear mixed models for species richness and abundance and network metrics.

Table S2. Statistical results from linear mixed models for species indices of seeds and rodents and network metrics.

Table S3. Relationships between species richness and abundance of seed and tree.

Fig. S1. Illustrations of seed traps, infrared (IR) camera and seed tagging method for measuring seed-rodent interaction strength.

SUPPORTING INFORMATION

Table S1. Statistical results from linear mixed models for species richness and abundance and network metrics: the model used stand age and patch size as fixed factors, and year as a random factor. MRA, metabolic rodent abundance; MSA, metabolic seed abundance; PCSA, per capita seed availability (PCSA= seed abundance/ rodent abundance); MPCSA, metabolic per capita seed availability (MPCSA= MSA/MRA). Fixed factors in bold indicate significant differences ($P < 0.05$).The datum of tree richness and abundance come from Zhao *et al*. (2016).

Items	Stand age			Patch size		
	d.f	*F*	*P*	d.f.	*F*	*P*
Species indices						
Rodent richness	**2, 33**	**9.97**	**<0.001**	1, 33	3.54	0.069
Rodent abundance	**2, 33**	**9.77**	**<0.001**	1, 33	1.92	0.175
MRA	**2, 33**	**4.59**	**0.017**	1, 33	1.74	0.196
Seed richness	**2, 33**	**18.25**	**<0.001**	1, 33	0.25	0.619
Seed abundance	2, 31	0.81	0.452	1, 31	2.25	0.144
MSA	2, 31	1.97	0.157	1, 31	1.56	0.221
PCSA	**2, 31**	**3.91**	**0.031**	1, 31	2.41	0.130
MPCSA	**2, 31**	**7.33**	**0.002**	1, 31	0.84	0.367
Tree richness	**2, 33**	**11.4**	**<0.001**	1, 33	0.63	0.432
Tree abundance	**2, 33**	**46.44**	**<0.001**	1, 33	3.04	0.090
Network metrics						
Connectance	**2, 31**	**3.93**	**0.030**	1, 31	0.66	0.424
Links per species	2, 31	0.03	0.974	1, 31	2.88	0.099
Nestedness	**2, 22**	**8.05**	**0.002**	1, 22	0.11	0.747
Weighted nestedness	2, 31	0.13	0.874	1, 31	0.74	0.393
Interaction strength	**2, 31**	**3.82**	**0.033**	1, 31	0.41	0.529

737 Table S2. Statistical results from linear mixed models for species indices of seeds and
738 rodents and network metrics. First models used species indices of rodent richness,
739 rodent abundance, seed richness and seed abundance as fixed factors and year as a
740 random factor; second model used per capita seed availability (PCSA= seed
741 abundance/ rodent abundance) as a fixed factor and year as a random factor; third
742 model used metabolic rodent abundance (MRA) and metabolic seed abundance (MSA)
743 as fixed factors and year as a random factor; and the last model used metabolic per
744 capita seed availability (MPCSA= MSA/MRA) as a fixed factor and year as a random
745 factor. Fixed factors in bold indicate significant differences ($P < 0.05$).

Fixed factors	Estimate± SD	df	t	P
Connectance				
Rodent richness	-0.204±0.112	32	-1.814	0.079
Rodent abundance	**0.189±0.087**	**31**	**2.158**	**0.039**
Seed richness	-0.054±0.057	30	-0.950	0.350
Seed abundance	-0.058±0.030	32	-1.966	0.058
PCSA	-0.018±0.012	35	-1.467	0.151
MRA	0.076±0.043	33	1.781	0.084
MSA	**-0.271±0.083**	**33**	**-3.274**	**0.002**
MPCSA	**-0.101±0.044**	**35**	**-2.282**	**0.039**
Links per species				
Rodent richness	-0.163±0.227	31	-0.717	0.479
Rodent abundance	0.049±0.176	30	0.277	0.784
Seed richness	0.008±0.114	30	0.071	0.944
Seed abundance	0.099±0.061	31	1.629	0.113

PCSA	0.041±0.023	34	1.789	0.083
MRA	-0.078±0.094	32	-0.829	0.413
MSA	0.132±0.186	33	0.708	0.484
MPCSA	0.083±0.090	34	0.917	0.366
Nestedness				
Rodent richness	7.381±6.651	21	1.110	0.280
Rodent abundance	**-1.135±0.504**	**21**	**-2.251**	**0.035**
Seed richness	**3.157±1.041**	**21**	**3.033**	**0.006**
Seed abundance	1.515±1.816	21	0.835	0.413
PCSA	0.368±0.678	24	0.543	0.592
MRA	-5.238±2.614	23	-2.003	0.057
MSA	-1.731±7.272	23	-0.238	0.814
MPCSA	5.007±2.603	24	1.924	0.066
Interaction strength				
Rodent richness	-0.182±0.151	31	-1.207	0.237
Rodent abundance	**0.284±0.117**	**31**	**2.430**	**0.021**
Seed richness	-0.108±0.076	30	-1.421	0.166
Seed abundance	-0.015±0.040	31	-0.384	0.704
PCSA	-0.017±0.017	34	-1.007	0.321
MRA	**0.151±0.163**	**33**	**2.403**	**0.022**
MSA	-0.082±0.124	33	-0.655	0.517
MPCSA	**-0.144±0.061**	**34**	**-2.361**	**0.024**

Weighted nestedness				
Rodent richness	0.139±0.402	31	0.346	0.731
Rodent abundance	0.111±0.312	31	0.357	0.724
Seed richness	0.173±0.204	30	0.847	0.404
Seed abundance	0.115±0.107	32	1.080	0.288
PCSA	0.030±0.041	34	0.727	0.472
MRA	-0.022±0.130	33	-0.169	0.867
MSA	**1.123±0.255**	**34**	**4.408**	**<0.001**
MPCSA	0.143±0.156	34	0.915	0.367

Table S3. Relationships between species richness (log-10 scale) and abundance (log-10 scale) of seed and tree. *, **, *** indicate $P < 0.05$, 0.01, 0.001, respectively. The data of tree richness and abundance was obtained from Zhao *et al*. (2016).

Items	Seed abundance	Tree richness	Tree abundance
Seed richness	-0.042	0.71***	0.42**
Seed abundance		0.13	0.36*
Tree richness			0.55***

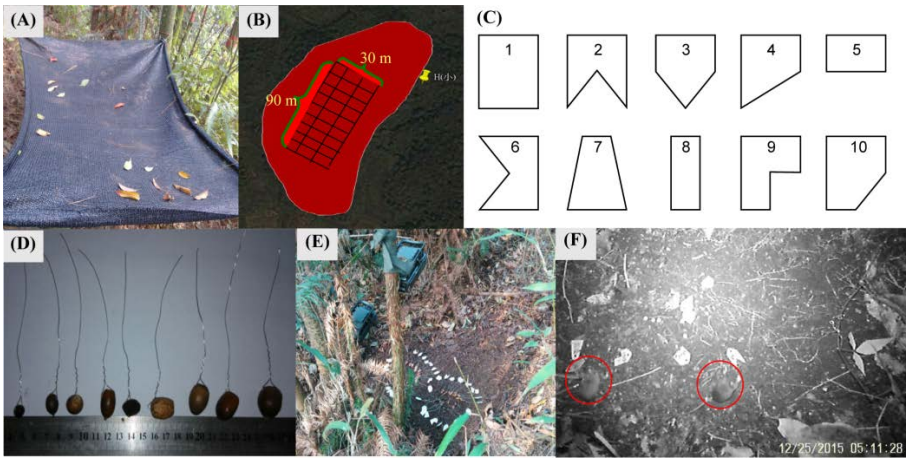

Fig. S1. Illustrations of seed traps, infrared (IR) camera and seed tagging method for measuring seed-rodent interaction strength. (A) seed trap. (B) Rodent trap grids. (C) Shapes of seed tags. Each shape was used to mark different individuals within a seed species. (D) Released tagged seeds. (E) Setting of IR camera traps nearby the seed station. (F) Two rodent individuals (*Apodemus draco*) recorded by an infrared camera.

Reference

Zhao, Q., Gu, H., Yan, C., Cao, K. & Zhang, Z. (2016). Impact of forest fragmentation on rodent-seed network. *Acta Theriologica Sinica*, 36, 15-23. (in Chinese with English summary)